DEVELOPMENT OF A POPULATION MODEL FOR HUMPBACK CHUB (Gila cypha) IN GRAND CANYON

Program Element I. A Feasibility Evaluation Completion Report

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SUMMARY

The feasibility of developing and implementing a population model for the endangered humpback chub (Gila cypha) in Grand Canyon was evaluated as part of the Glen Canyon Environmental Studies (GCES). We determined that, for humpback chub in Grand Canyon, age-structured models would be more useful than simple birth-death models, primarily because factors affecting humpback chub differ by age group. A modelling effort will be a valuable tool to identify and integrate existing data; identify and quantify important state and rate variables such as reproduction, recruitment, and survivorship; identify and evaluate population and environmental parameters that most affect change; help guide and interpret monitoring; evaluate population viability; and provide insight to population behavior under adaptive management. The framework for the model can serve as an organizational tool for data integration to assist the GCES Scientific Information Management System (SIMS), and the process of model development can help organize and develop the Integrated Humpback Chub Final Report. A comprehensive model can help guide the Long-Term Monitoring Plan, and can provide insight to the behavior of the population under adaptive management of Glen Canyon Dam.

This program element is the first of five elements identified as the population modelling program for humpback chub in Grand Canyon, and described in this document. We recommend proceeding with Element II--Develop a Conceptual Population Model. This next element will solicit input and consensus from Grand Canyon researchers on a conceptual population model, and will initiate the process of data assimilation and developing mathematical relationships.

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INTRODUCTION

The purpose of this document is to assess the feasibility of developing and implementing a population model for humpback chub (Gila cypha), as part of the Glen Canyon Environmental Studies (GCES). This Completion Report satisfies the first of five program elements identified as a modelling program for humpback chub, and provides a framework and recommendations for performance of the four remaining program elements. This report also provides a background for GCES humpback chub studies in Grand Canyon, and a description of the population modelling program.

Integrated GCES Investigations

The need for a population model was identified by the Aquatic Coordination Team (ACT) of GCES, and is inherent to the overall purpose and objectives of the humpback chub studies in Grand Canyon. The purpose of the integrated GCES investigations is to:

Determine the ecological and limiting factors of all life stages of humpback chub in the Colorado River, Grand Canyon, and the effects of Glen Canyon Dam operations.

The objectives of the integrated GCES investigations are to:

- Determine resource availability and use (habitat, water quality, food, etc.).
- Determine reproductive capacity and success.
- Determine survivorship of early life stages.
- Determine distribution, abundance and movement, and effects of dam operations.
- Determine important biotic interactions with other species.
- Develop a population model from empirical data.

Comprehensive studies of the life history and ecology of the humpback chub in Grand Canyon are being conducted under Phase II of GCES. These investigations are designed to provide input to state and federal agencies charged with management and protection of this endangered species, and to address two of seven conservation measures arising from the 1978 Biological Opinion on Glen Canyon Dam operations. Additional studies are likely to

be implemented in 1995, after the Glen Canyon Dam Environmental Impact Statement (GCDEIS) and Biological Opinion become Record of Decision.

Mainstem investigations are being conducted by BIO/WEST, Inc. (Valdez et al. 1992, Valdez and Hugentobler 1993, Valdez 1994) and Arizona Game and Fish Department (Angradi et al. 1992a, Arizona Game and Fish Department 1994), while studies in the Little Colorado River (LCR) are by Arizona State University (Douglas and Marsh 1992, 1993), Arizona Game and Fish Department (Angradi et al. 1992b, Arizona Game and Fish Department 1994), and U.S. Fish and Wildlife Service (Gorman 1994).

Purpose and Objectives of Modelling Program

The purpose identified in this document for the modelling program is to provide an integrated quantitative characterization of the humpback chub population in Grand Canyon, as well as a tool to evaluate population behavior. The objectives of the modelling program are to:

- Provide the framework for a comprehensive assimilation and integration of data and information for humpback chub in Grand Canyon.
- Provide a tool to help understand humpback chub population dynamics and environmental interrelationships.
- Identify missing life history information as guidance to core research.
- Evaluate efficacy of long-term monitoring.

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MODELLING PROGRAM OVERVIEW

Role of Models

The role of models varies with program objectives and goals. Modelling programs are best used as tools to:

- Help researchers and decision-makers define problems and organize thoughts (Starfield and Bleloch 1986).
- Quantify factors that are not easily or directly measurable (Vaughan and Saila 1976).
- Integrate factors to assess their effects on system dynamics (Forrester 1961).
- Examine the consequences of complexity (Thornley and Johnson 1990).

These tools are best utilized along with laboratory and field experimentation in the problem solving/decision-making process (Beyschlag et al. 1994). While models allow for investigation and integration of system dynamics, their outputs are of minimal value unless they can be supported or validated by at least some findings from direct measurement.

The role of modelling for humpback chub in Grand Canyon is primarily as an organizing and integrating tool to assist research, integration, and monitoring efforts. A modelling effort will provide the framework for data integration, identify additional research needs, provide guidance to long-term monitoring, and act as an organizational tool for the Integrated Humpback Chub (HBC) Final Report (Figure 1). It could be used as a predictor of population dynamics, depending on the reliability of data input.

Approaches To Modelling

Population studies are usually approached in one of three ways (Smith and Fowler 1981). The first is a natural history study, which is primarily descriptive in nature, and best describes much of the work on humpback chub, to date. Descriptive information is essential to defining a population, its distribution, and basic ecology, and to formulate concepts on the dynamics of the population. The second approach is development of conceptual models which are usually compartmental flow diagrams accompanied by written narrative. These conceptual models are designed to visualize interrelationships of various components of the population with the environment. The third approach is to develop formal mathematical

GLEN CANYON ENVIRONMENTAL STUDIES ENDANGERED FISH RESEARCH FLOW CHART GCDEIS **GCDEIS** INFORMATION ADDITIONAL STUDIES SPECIFIC TO **ALTERNATIVES** ASU FINAL PHINCHAL INVESTIGATORS HITEGRATION TEAM HBC FILIAL REPORT BIO/WEST FINAL INTEGRATED PATA SHARING AGFD USFWS POPULATION MCDELLING **PROGRAM** HISTORIC AND CURRENT GCES GRAND CANYON DATABASE DATABASE AND LONG-TERM MONITORING DEVELOPMENT LONG-TERM MONITORING AND ADDITIONAL STUDIES OTHER GCES '94 '93 '97 '92 '96 '95 YEAR

Figure 1. Flow chart of Glen Canyon Environmental Studies Endangered Fish Research Program illustrating the inclusion of a modelling program.

models to describe population components and functions, and their dynamics. All three approaches overlap, to some extent, and a holistic approach to the study of population dynamics involves the integration of all three. This integrated approach is recommended for humpback chub in Grand Canyon, in which conceptual and mathematical models will be developed from past and present life history information on humpback chub in Grand Canyon, as well as other populations.

Suitability of Modelling Program to Humpback Chub

Of the four mainstem Colorado River endangered fish species--Colorado squawfish (<u>Ptychocheilus lucius</u>), razorback sucker (<u>Xyrauchen texanus</u>), bonytail (<u>Gila elegans</u>) and humpback chub--the humpback chub in Grand Canyon is best suited for development of conceptual and mathematical population models for the following reasons:

- The species is relatively accessible for study, and sample methods have been developed and refined for reliably capturing all life stages.
- Much research has been conducted on this species, prior to and including the present studies, and a sizable database exists for identifying parameters and interactions.
- Humpback chub in Grand Canyon, as in other populations, exhibit a high fidelity for a relatively small geographic region that permits use of closedsystems analyses, and minimizes problems with random immigration and emigration.
- The life history of humpback chub is similar to that of many freshwater forms, and strategies and results of prior modelling efforts can be applied.

This population model for humpback chub in Grand Canyon will consist of a series of linked mathematical and logical relationships that can be used to provide inferences into various aspects of the population. We do not expect that any aspect of this model can or will be used to precisely describe or predict specific elements of the population. Instead, this population model is expected to provide insight into the relationships between various population parameters and the environment, and the behavior of the population over time. The model can also be used to aid in estimation of parameters and rates that are difficult to measure.

PROGRAM ELEMENTS

Modelling efforts are often conducted as a series of work elements, in which performance of one can depend upon completion of previous elements. This stepwise approach allows for periodic and regular evaluation of suitability and appropriateness of a modelling program for a particular species, and provides useful interim products throughout the modelling effort. Once developed, these models can be used to identify needed core research, guide and interpret monitoring data, and evaluate population viability. We recommend the following five program elements as the organizational framework for this population modelling program:

- I. Conduct a feasibility evaluation.
- II. Develop a conceptual population model.
- III. Identify and assimilate data for important state and rate variables.
- IV. Develop a series of mathematical and logical relationships.
- V. Develop and implement a population model.

Completion of each element identified above is dependent on completion of previous elements. The time frame for these relative to the BIO/WEST Final Report and Database Integration, is shown in Figure 2.

The first program element evaluates the feasibility of developing a model for this population (this Completion Report). The second will develop and refine a compartmental conceptual model. The third will identify and assimilate information for important state and rate variables, and the fourth will develop a series of mathematical and logical relationships that lead to the fifth element, or the population model.

Element I. Conduct a Feasibility Evaluation

This report constitutes the feasibility evaluation for a modelling program for humpback chub in Grand Canyon. The purpose of this evaluation was to assess the feasibility of developing and implementing a population model for humpback chub in Grand Canyon. The objectives of the evaluation were to:

- 1. Identify the need for a population model.
- 2. Determine the suitability of known information for a population model.

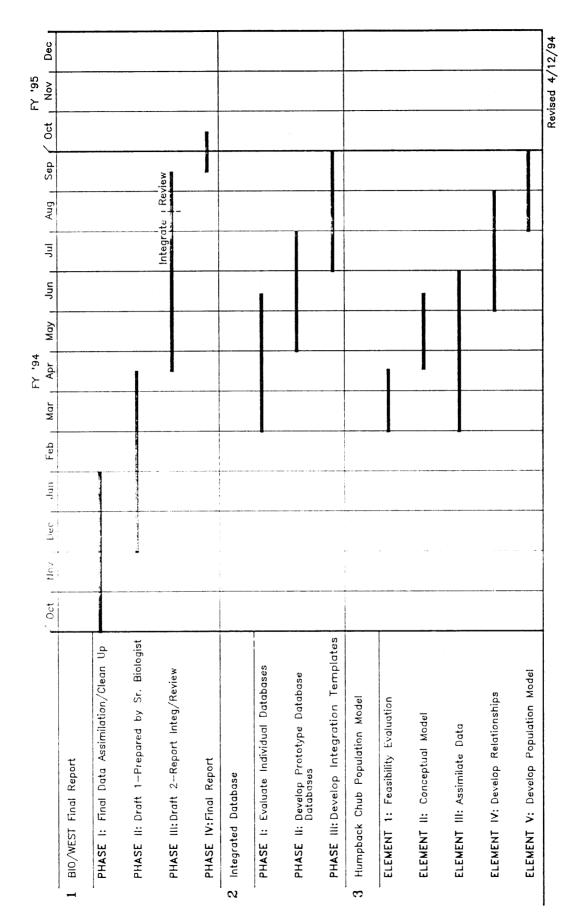


Figure 2. BIO/WEST schedule for Final Report, Integrated Database, and Population Model.

- 3. Identify appropriate models and approaches according to data type and availability, as well as known population characteristics.
- 4. Describe roles of models in integrating research and monitoring.
- 5. Refine general population modelling approach for humpback chub.

The modelling program was determined feasible and recommended, primarily on the basis of available past and present data on the population. Population size and distribution, and individual movement are sufficiently understood to allow for a reasonable definition of the population. Although all state and rate functions are not known, more data are available for demographics of humpback chub in Grand Canyon than for any other native mainstem species of the Colorado River.

Element II. Develop A Conceptual Population Model

The purpose of a conceptual model is to provide a visual representation of state and rate variables of the population. The objectives of the conceptual model are to:

- 1. Develop a compartmental representation of perceived state and rate variables of the population.
- 2. Refine the conceptual model through input from other researchers.
- 3. Solicit data and information from other researcher on important state and rate variables.
- 4. Provide a framework for the infrastructure of the population and interrelationships to the environment.

This conceptual model will be designed to provide a compartmental representation of the present understanding of humpback chub in Grand Canyon. Important parameters are the estimated numbers of individuals in various age groups (state variables) within defined components of the system, and reproductive, survival, and movement rates (rate variables) between these components. A conceptual model does not contain values for the state or rate variables, but simply identifies the parameters and interrelationships within the population, as well as abiotic and biotic factors affecting each variable.

The conceptual model will be reviewed and refined with input from past and present researchers of humpback chub in Grand Canyon. This model will provide the organizational

framework to help assess the current knowledge of the population, identify missing data, and identify rate and state variables that may affect the greatest change in the population. The framework may change with new information or needs from managers and decision-makers. This conceptual model will be extremely useful in integrating information collected by past and present researchers in Grand Canyon, and to help organize and assess the status of data collected for all GCES project objectives.

The conceptual model also provides the framework for a quantitative modelling effort. While mathematical formulations rarely include entire conceptual models, this consensus picture of the population is essential in identifying and developing important mathematical relationships.

Element III. Identify And Assimilate Data for Important State and Rate Variables

The purpose for identifying and assimilating information for important state and rate variables is to assess availability and types of data needed for definition of variables such as cohort size, survival, growth, recruitment, reproductive success, etc. The objectives of the element are to:

- 1. Identify important state and rate variables.
- 2. Assimilate empirical data for important state and rate variables.
- 3. Identify missing and needed information.

Important state and rate variables will be identified with the aid of the conceptual model, input from Grand Canyon researchers, and known life history information on humpback chub. This process will be used to prioritize data searches and analyses for developing and presenting these variables. Empirical data will be used from field or laboratory measures, where available, and literature will be researched for similar species to fill data needs. Where data are missing for important variables, Grand Canyon researchers will be asked, through a Delphi approach, to provide best estimates.

Alternately, life history parameters that are difficult to measure can be estimated using preliminary model results. With information on some life history parameters, others can be estimated using a model with stated assumptions of population trajectory (Vaughan and Saila 1976, Van Winkle et al. 1978, Deangelis et al. 1980, Manly 1990). For example, if estimated adult population size and survival rates are known, the recruitment rate needed

to maintain a stable, or increasing, population can be calculated. Such calculated rates can be compared with estimates from field measurements to determine if recruitment is sufficient to maintain the population, and to assess the effect of high variation in recruitment on population dynamics. Significant deficiencies in important parametric data may result in recommendations for future research efforts.

Also, rate functions affected by density of some aspect of the population (density dependence) may be identified with a model (Van Winkle et al. 1978, Manly 1990). For example, the robust condition of adult chubs in the mainstem Colorado River suggests that factors affecting survival of younger age groups (perhaps density) may be limiting the number of fish that reach maturity as hypothesized for many fish by Gulland (1965).

Element IV. Develop A Series of Mathematical and Logical Relationships

The purpose for this element is to integrate the assimilated information on humpback chub from Grand Canyon into a series of mathematical and logical relationships. The objectives of the element are to:

- 1. Analyze data for describing important state and rate variables.
- 2. Identify parameters that most affect changes in the population.
- 3. Assess available and missing information on state and rate variables.

Data assimilated under Element III will be synthesized and analyzed to provide mathematical or logical relationships for important state and rate variables. Many databases from Grand Canyon do not contain the type of information necessary for population modelling. Some state and rate variables can be gleaned from existing data through analysis and interpretation, which are best performed by investigators responsible for initial data collection, and may be provided in progress reports. This modelling program will work with researchers to provide guidance in data analyses necessary for model input.

The relative change in potential population growth rate caused by changes in life history parameters can be effectively assessed with population models (Horst 1977, Caswell 1978, Caswell 1988). This "sensitivity analysis" will help focus the monitoring effort by identifying key monitoring parameters to ascertain the status and trajectory of the population. In addition, it will help identify life history parameters that may have the biggest effect on the population in response to environmental change. This may include

investigating environmental changes that have detrimental effects (e.g., reducing food supply, increasing predation), or management schemes that may prove beneficial to the population (e.g., temperature and flow modifications, predator reduction).

This element will also help to identify missing information on important state and rate variables, which may not become evident until attempts are made to integrate analyzed data. Differences in data collection methods, spatial or temporal discrepancies, or data-type mismatches may preclude integration of certain data partitions into a comprehensive modelling program.

Element V. Develop and Implement a Population Model

The information assimilated under Element IV will be integrated into a population model for humpback chub in Grand Canyon. This element will develop primarily agestructured models, with model formulation that meet each of the program objectives, and provide parameter estimation needs and monitoring data evaluation.

The results of this program element will be presented, together with a summary of previous elements and results, in a Final Report. This report will contain a background description of program objectives and modelling approaches, a summary of program elements and results, and a narrative on the population model and associated mathematical and logical relationships, along with a hardcopy and computer diskette with these relationships.

Other Possible Model Applications

At least two additional applications are identified for a population model of humpback chub in Grand Canyon:

- 1. Guide and interpret long-term monitoring.
- 2. Population viability analysis.

These have not been identified as specific program elements because implementation of the population model for these and other applications will depend on model suitability and appropriateness of model application to various program objectives, such as the long-term monitoring plan. Similarly, a population viability analysis may or may not be appropriate or necessary, depending on the objectives of recovery program elements for humpback chub in Grand Canyon.

Guide and Interpret Long-Term Monitoring

A long-term monitoring plan has been identified as an important aspect of adaptive management of Glen Canyon Dam. This population model could provide guidance for the plan, and aid in data interpretation. Monitoring activities will realistically be limited to parameters that are readily measurable, but not likely to totally portray population trajectory. Population modelling will provide one way to interrelate monitoring parameters with population status.

The combined endeavor of linking the modelling effort with the monitoring program, will provide a better assessment of population status and the means to modify the monitoring program, as well as identify areas needed for further research. This will be particularly useful when monitoring results do not fit expected model outputs, based on the present level of understanding of the population. Model formulations can be used to identify important measurable parameters, and to compare these with field validation data from long-term monitoring.

Population Viability Analysis

The analysis of species viability-or vulnerability to extinction--is rooted in the theory of island biography (MacArthur and Wilson 1963,1967), which contends that persistence of plant and animal species is related to island size. This theory became the basis for later work in defining refuge sizes (Diamond 1976, Diamond and May 1981, Soulé 1987). The probability of species persistence has been assessed for whole systems (Forman et al. 1976, Lovejoy 1980), as well as individual populations (Frankel and Soulé 1981, Shaffer 1981). Persistence of whole systems and individual populations are generally interrelated, and key species are sometimes used to assess the viability of whole systems (Frankel and Soulé 1981, Soulé and Simberloff 1986). Population viability could be used to assess the probable success of a second spawning population of humpback chub in Grand Canyon, as well as its effects on the existing population.

The vulnerability of a population is often expressed as the minimum viable population (Soulé 1987) that would have a high probability of surviving for a long period of time, e.g., a 95% probability that the population survives for 1000 years (Allen et al. 1992). Because species have different life history strategies, the minimum viable population size, and number

and sizes of refuges is not easily generalized (Simberloff and Abele 1976, Simberloff and Abele 1982, Soulé 1987).

Shaffer (1981) listed four sources of uncertainty that affect population viability:

- Demographic uncertainty.
- Environmental uncertainty.
- Natural catastrophes.
- Genetic uncertainty.

Demographic uncertainty of humpback chub would result from random changes in survival, recruitment, and population distribution. Environmental uncertainty would result from changes in food supply, populations of competing or predatory fishes, parasite infestation, and water flow regimes from Glen Canyon Dam and the LCR (as flows affect water temperature, turbidity and volume). Catastrophes affecting chub populations may include the release of toxic chemicals into the river system, introduction of a deadly disease or debilitating parasite, and major storm events that cause significant habitat changes. Genetic uncertainties result from changes in gene pool caused by genetic drift, and inbreeding that may affect reproductive or survival rates.

Environmental (Allen et al. 1992, Shaffer 1987) and demographic uncertainties--as related to population distribution and connectivity (Gilpin 1987)--are the most likely factors affecting the persistence of humpback chub in Grand Canyon, although catastrophic uncertainty can not be discounted. Modelling efforts to assess population viability should include investigating the effects of demographic and environmental uncertainties, as well effects of catastrophic events. Genetic uncertainty is unlikely to affect the present humpback chub population in Grand Canyon, because of the absence of congeneric species (i.e., roundtail chub, <u>Gila robusta</u>, and bonytail, <u>Gila elegans</u>), and because present population size likely exceeds that considered necessary for maintaining genetic diversity (Frankel and Soulé 1981, Franklin 1980).

TYPES OF MODELS

The formalization of conceptual models into mathematical entities generally produces one of two basic types of fish population models:

- Simple birth-death models.
- Age- and stage-structured models.

Both can be structured as deterministic (non-random) or stochastic (random components) models and can include the effects of density on various rates. Each of these model types is evaluated for its applicability in modelling humpback chub population dynamics to meet the stated objectives.

Simple Birth-Death Models

These models characterize the rate of change in population size in terms of average population birth and death rates (Renshaw 1990). The population can be characterized by unbounded growth or decline, or its growth rate can be limited by the feedback of densityas in the familiar logistic population growth model. These models are characterized by the lack of any age structure, and assume average rates of reproduction and survival across the entire population. Time lags are often built into these models in an attempt to account for lengthy maturation times (Goel et al. 1971, Braddock and Van Den Driessche 1981). These models are most applicable when all life stages of a species are subject to similar ecological pressures.

The uses of this model formulation are varied and widespread ranging from characterizing population growth or decline of many organisms (Goel et al. 1971, Starfield and Bleloch 1986, Renshaw 1990) to calculating persistence times in viability analyses (Leigh 1981, Belovshy 1987, Allen et al. 1992). One significant use of these models in fisheries is development of catch-based models for harvested fish populations (Gulland 1983, Schnute 1985). Stock-recruitment or surplus-yield models have been significant components of fisheries management based on the assumption of density-limiting population growth (e.g., Ricker 1973, Getz 1980, 1984, Gatto and Rinaldi 1980, Walter 1981, Fowler et al. 1982, Policansky 1986).

Use of simple birth-death models is limited in characterizing humpback chub populations to meet program objectives. The major drawback is the inability to separate life

stages into individual units that often behave differently and are subject to different ecological needs and environmental conditions. In addition the large body of catch-based models, applied to harvested fish populations, has limited value is assessing the humpback chub population. However, these birth-death models may be used to assess dynamics of specific age groups of chubs, and in a general way, to assess population persistence.

Age- and Stage-Structured Models

Age- and stage-structured models have their foundations in the work of Bernardelli (1941), Lewis (1942) and Leslie (1945). These models are based on division of a population into distinct age, size, or stage classes, and allow for assessment of population dynamics assuming different reproductive and survival rates for each class. They were developed for populations with age- or stage-specific differences between classes.

The simplest form of these models are projection (Leslie) matrices used to calculate population size in each of **m** age groups in time **t**+1 from the population in time **t** (Figure 3). The square projection matrix A contains rates of reproduction and survival for each of the **m** age groups. The model structure has been modified slightly to account for stage-based populations—those whose structure are more readily assessed by size or developmental stage instead of age (Letkovitch 1965, Caswell 1982, 1988).

These models have been refined substantially since their original formulation (Usher 1972). The application of these models has assumed that rates in the projection matrix are stochastic in nature (Pollard 1966, Getz and Haight 1989), functions of density (Leslie 1948, 1959, Smith 1973, Pennycuick 1969, Fowler 1987), and functions of environmental factors (Horst 1977, Vaughan 1981). The flexibility of this modelling structure is in the ability to make each element of the projection matrix a function of any factor affecting it.

Age- and stage-based models have been used for a variety of organisms, including insects (Lefkovich 1965, Horst 1976), large mammals (Fowler and Smith 1973, Ryel 1980, Fowler 1981), and trees and herbaceous species (Hartshorn 1975, Meagher 1982, Law 1983). Fish populations have also been assessed with these models to assess harvest yield (Walters 1969, Jensen 1974, Quinn 1981, Law and Grey 1988), to quantify effects of environmental factors (Horst 1977, Vaughan 1981), to estimate life history parameters (Vaughan and Saila

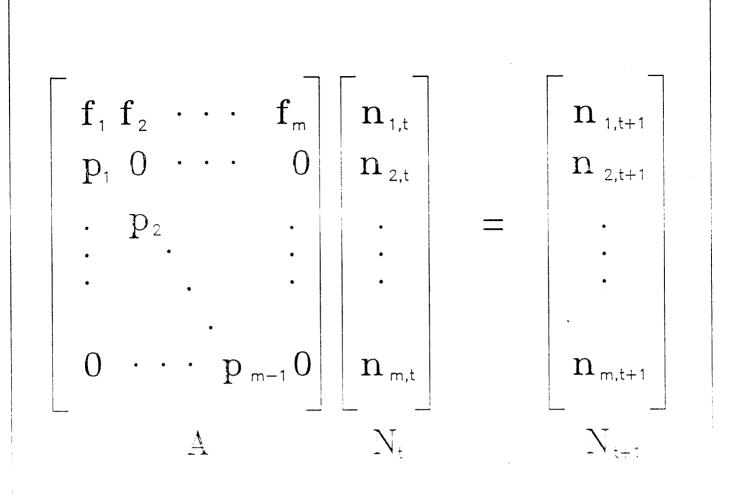


Figure 3. Projection matrix model for calculating the population of a species at time t+1 (N_{i+1}) from the population at time t (N_i) using the projection matrix A (from Fowler and Ryel 1978).

1976, Van Winkle et al. 1978), and to evaluate the significance of changes in life history on population growth rate (Caswell et al. 1984).

The age-structured model formulation would be the most useful in a modelling effort of humpback chub in Grand Canyon. The model format readily adapts to a conceptual model framework, and past and present studies will provide initial estimates of many of the model parameters. Environmental and density-dependent effects on various parameters can readily be incorporated into the model structure.

A complete model formulation for humpback chub in Grand Canyon--including parameter estimation of all the state and rate variables--is unlikely. Instead, formulations will be based on needs, objectives and to some extent on available data. Thus, a general formulation of the population used in viability or sensitivity analyses, may contain much of the structure included in a conceptual model, while a much reduced formulation may be used to estimate parameter values, or assess certain monitoring data where only a segment of the population is of interest.

PARAMETER ESTIMATION

Parameterization of an age-structured model for humpback chub in Grand Canyon should be possible with the volume of data available and being collected. As mentioned above, past and present research has accumulated a sizeable database on life history parameters of humpback chub in Grand Canyon, as well as from five other populations (Black Rocks, Westwater Canyon, Desolation Canyon, Cataract Canyon, and Yampa Canyon). While this database will not provide estimates for all parameters identified in a conceptual model, it will likely provide much of the needed information.

Parameter needs for an age-structured model fall into four basic categories:

- Age-class population size.
- Age-specific survival rates.
- Age-specific reproductive rates.
- Age-specific and spatially-determined rates of movement (immigration and emigration).

Studies in both the mainstem Colorado River and the LCR should supply information on many of these parameters. Mainstem tagging studies may provide estimates of population size, as well as survival and fecundity rates of adults and subadults living in the mainstem. In addition, sex ratios of these fish can be calculated. Tagging studies should provide estimates of population size, sex ratio, and survival and fecundity rates of subadult and adult chubs in the LCR. The combination of data from the LCR and mainstem should provide an estimate of the exchange of fish between the two systems. Movement rates of subadult and adult humpback chub in the mainstem downstream of the LCR component may be assessed, but estimation of population size and survival and reproductive rates may be difficult.

Assessing abundance of younger chubs is likely to be more difficult. However, within the LCR, estimates of population size and survival may be possible through tagging studies-at least for individuals greater than 150 mm total length. In addition, the rate of emigration from the LCR may be possible through coordinated efforts between the LCR and mainstem

studies. Estimates of survival and movement in the mainstem may also be possible through tagging studies.

The effects of environmental changes on life-history parameters will be difficult to measure directly in most circumstances. However, such changes in parameter values can be investigated by hypothesizing bounds on the parameter value as affected by environmental change. These exercises are often beneficial to assess relative magnitude of an environmental change or perturbation.

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RECOMMENDATIONS

- 1. Familiarize Grand Canyon researchers with this modelling program by providing this Completion Report for Project Element I Feasibility Evaluation.
- 2. Solicit input from Grand Canyon researchers for refinement of a conceptual compartmental model.
- 3. Request data and information input from Grand Canyon researchers for important state and rate variables.
- 4. Proceed with Project Element II (Conceptual Population Model) of the modelling program.
- 5. Provide a mechanism for evaluating the effectiveness of each program element to the GCES program during the modelling program.
- 6. Integrate the modelling effort into helping to determine future data needs, core research needs, and as guidance for long-term monitoring.
- 7. Use an age- or stage-based population model structure in modelling efforts on humpback chub.
- 8. Conduct a viability analysis for humpback chub in Grand Canyon after Program Elements I-V are completed. Include in this analysis, the effects of different environmental changes and perturbations, and the significance of adding a second spawning population.

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